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# *MICROVELIA POLHEMI,* N. SP. (HETEROPTERA: VELIIDAE) FROM DOMINICAN AMBER: THE FIRST FOSSIL RECORD OF A PHYTOTELMIC WATER STRIDER

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*Abstract.*—A fossil water strider, *Microvelia polhemi* n. sp., is described from the Oligo-Miocene Dominican amber based upon a single macropterous male. This is the first fossil record of the genus *Microvelia* (Microveliinae, Veliidae), one of the most common and widespread genera of semiaquatic bugs (Gerromorpha). Several characters, in particular the striking, white basal markings of the fore wings, affiliate the fossil species with the extant *Microvelia laesslei* Drake and Hussey from Jamaica. The latter belongs to a guild of Neotropical veliids living in phytotelmic habitats, especially pockets of rain-water accumulated between the leaf axils of plants belonging to the family Bromeliaceae. The fossil species may have used the same type of habitat in the Dominican amber forest.

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Semiaquatic bugs or water striders (Hemiptera-Heteroptera, infraorder Gerromorpha) are common insects found on water surfaces in freshwater and marine habitats throughout the world (Andersen 1982). Limnic habitats range from large, permanent water bodies (lakes, ponds, rivers, and streams) to small temporary pools or streams. A special type of habitat occupied by water striders is water accumulating in natural containers such as treeholes, bamboo internodes, and water-filled parts of epiphytic plants (collectively called phytotelma; see Wesenberg-Lund, 1943). Most species living in these natural containers are never found in other types of limnic habitats (Andersen, 1982; Polhemus and Polhemus 1991; Polhemus and Copeland, 1996; Yang and Kovac, 1995).

The large amber deposits from the Dominican Republic (Hispaniola, Greater Antilles) are renowned for the taxonomic diversity and preservation quality of their insect inclusions. Most Dominican amber insects belong to terrestrial groups (Poinar, 1992; Grimaldi, 1996), but a few aquatic insects have been described, including the water striders *Electrobates spinipes* Andersen and Poinar (1992) (Gerridae, Electrobatinae) and *Halovelia electrodominica* Andersen and Poinar (1998) (Veliidae, Haloveliinae). Based upon a macropterous male from Dominican amber, I here describe the first fossil species belonging to the water strider subfamily Microveliinae (Veliidae) and to the genus *Microvelia* Westwood (Andersen, 1998). This genus is at present distributed worldwide with more than 200 described species (Andersen, 1982).

The fossil species is named for John T. Polhemus in recognition of his outstanding and life-long contributions to our knowledge about the systematics, faunistics, and biology of aquatic and semiaquatic Hemiptera-Heteroptera of the World.

## MATERIAL AND METHODS

One veliid specimen (Figs. 1–2) enclosed in a piece of yellow amber weighting about 0.2 grams. The piece is rectangular with the greatest length = 9.5 mm, the

Fig. 1. *Microvelia polhemi* n. sp. Macropterous male holotype from Dominican amber, length 1.85 mm. (Photo G. Brovad, Zoological Museum, University of Copenhagen).

greatest width = 9 mm, and the greatest thickness = 3 mm. The amber piece containing the fossil originates from the El Valle area in the eastern part of the Dominican Republic. The exact age of the Dominican amber deposits is still not known, and estimates based on microfossil and $^{14}C$ analyses have produced a range from 15–30 myr (Grimaldi, 1995; Iturralde-Vincent and McPhee, 1996).

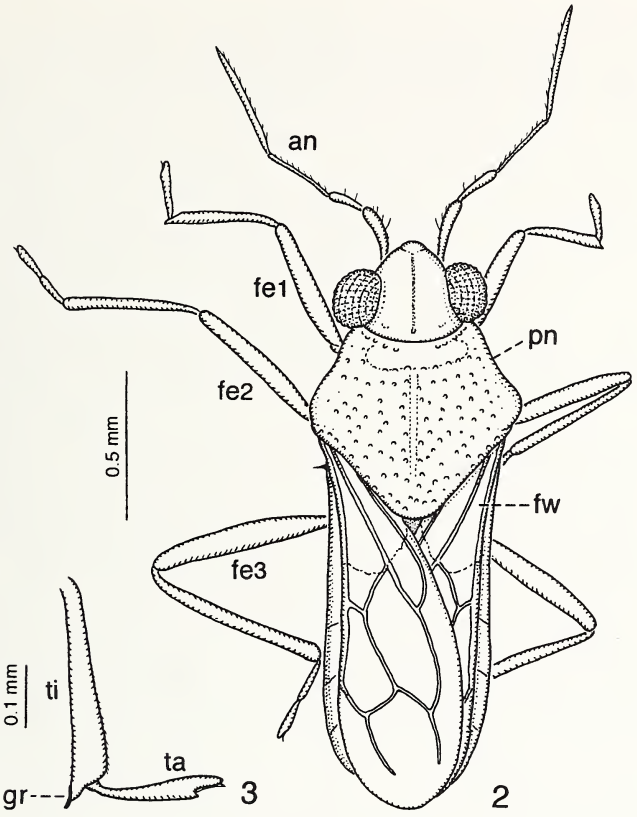
The piece is polished, highly transparent, with few impurities, cracks and fissures. The veliid is located superficially and plainly visible from above. All appendages are preserved *in situ*. The specimen was studied directly or by immersing the piece of amber in glycerin, using fiber optic reflected and incandescent transmitted light. All measurements are given in mm and were made using a ocular micrometer. Total length was measured from the tip of the head to the end of the abdomen. Measurements of antennal segments 3 and 4 include the basal internode. Lengths of the femora are measured along the anterior margin of the segments and do not include the trochanters.

## TAXONOMY

### **Microvelia polhemi**, new species

**Description.**

*Size: Holotype,* macropterous male, total length 1.85, maximum width 0.7.




Figs. 2–3. *Microvelia polhemi* n. sp. 2, dorsal habitus of macropterous male holotype *in situ.* 3, left fore tibia and tarsus of male. Abbreviations: an, antenna; fe1, fe2, fe3, fore, middle, and hind femora; fw, fore wing; gr, tibial grasping comb; pn, pronotum; ta, tarsus; ti, tibia.

*Color and vestiture:* Chiefly dark brownish above. Antennae brownish; antennal segments with scattered, semierect, short pubescence. Rostrum yellowish brown. Pronotum with a transverse, pale yellowish marking along anterior margin delimited by transverse rows of dark punctures in front and behind; additional blackish punctures are scattered all over pronotal lobe. Thorax furnished with short and oppressed pubescence. Legs chiefly yellowish brown, femora distally darkened; pubescence of leg segments chiefly short and oppressed. Fore wings chiefly brownish with slightly darker veins; basal third of each wing snowy-white. Ventral surface of thorax and abdomen brownish.

*Structure: Macropterous male* (Figs. 1–2) subovate, length about 2.7× greatest width across pronotum (1.83: 0.69). *Head* much shorter than wide across eyes (0.31: 0.48), slightly deflected anteriorly. Dorsal head surface with indistinct median, longitudinal impression and a small circular impression near the hind corner of each eye. Compound eyes globular, diameter about than half maximum width of interocular space (0.13: 0.30). Antennae long and slender, about 0.6× total length of insect

(1.03: 1.83), inserted obliquely below and close to eye margins; lengths of segments 1–4: 0.23, 0.15, 0.26, and 0.39; first segment curved, surpassing apex of head with more than half its own length, distinctly thicker than segments 2–4; second segment relatively short, slightly thicker than segments 3–4; third segment very slender; fourth segment long, fusiform. Rostrum slender, apex just surpassing posterior margin of prosternum; lengths of segments 1–4: 0.07, 0.04, 0.25, and 0.13. *Thorax.* Pronotum large, pentagonate, median length about 2× length of head (0.60: 0.31), maximum width (across humeral angles) slightly more than median length (0.69: 0.60); anterior margin of pronotum slightly concave, humeral angles prominent, slightly raised, posterior margin produced in middle, covering wing bases. Thoracic sterna subequal in length (0.20). Metasternum with posterior margin slightly produced in middle; median scent orifice indistinct, lateral scent channels curved forwards, ending on metacetabula with tufts of erect hairs. *Legs.* Lengths of leg segments (femur: tibia: tarsus): fore leg: 0.46, 0.39, and 0.21; middle leg: 0.51, 0.46, and 0.28; hind leg: 0.60, 0.60, and 0.29. Fore femora (Fig. 2, fe1) relatively slender (maximum width 0.8); fore tibia (Fig. 3, ti) widened distally, with a very short (0.04) grasping comb (gr) composed of densely set, row of minute, black spinous hairs on the inner surface towards apex; fore tarsus (ta) with a single segment. Middle femora (Fig. 2, fe2) about 0.3× length of insect, slender (width 0.07); tibiae slender and straight; middle tarsi with two segments measuring 0.13 and 0.15, respectively. Hind femora (fe3) slightly thickened (maximum width 0.09); hind tibiae distinctly longer than middle tibiae; hind tarsi with two segments measuring 0.13 and 0.16, respectively. Trochanters of all legs subequal in length (0.14–0.16). Claws small but distinct, inserted preapically on all tarsi. *Wings*: Fore wings (Fig. 2, fw) covering abdomen except connexiva; three longitudinal veins arising from base, branching and reuniting distally, forming four closed cells: two relatively narrow cells in basal part and two larger cells in median part of wings. *Abdomen* relatively long with ventral segmentation fairly distinct; median lengths of sternites 2–7: 0.13, 0.10, 0.10, 0.11, 0.14, and 0.21; abdominal venter slightly depressed, but otherwise not modified; genital segments relatively small (median length 0.20), slightly protruding from abdominal end; parameres not visible externally, presumably small and symmetrically developed.

**Types.** Holotype, macropterous ♂, contained in a piece of amber originating from the El Valle area in the eastern part of the Dominican Republic; holotype labelled as AMNH no. 10-324 and deposited in the American Museum of Natural History, New York, U.S.A.

**Distribution and geological background.** Dominican Republic, Hispaniola, Greater Antilles. Age 15–30 myr (Upper Oligocene–Lower Miocene).

## DISCUSSION

**Classification.** The following characters are important in assessing the taxonomic position of the fossil insect:

(1) Very small winged heteropterous insect, male length only 1.85 mm.
(2) Dorsal head surface with median, longitudinal impression.
(3) Eyes relatively large, diameter about half width of interocular space.

(4) Antennae relatively long and slender; first segment slightly shorter than third segment; second segment slightly shorter than third segment.
(5) Pronotum of macropterous form large, pentagonate, covering all of meso- and metanotum as well as the wing bases.
(6) Metasternum with lateral scent channels curving forwards and ending on metacetabula in a small tuft of hairs.
(7) Fore tibia of male with short grasping comb.
(8) Fore tarsi one-segmented, middle and hind tarsi two-segmented.
(9) Claws inserted before apex of last tarsal segment.
(10) Fore wings with few veins which form four closed cells.
(11) Fore wings with striking, snowy-white basal marks.
(12) Hind femora slightly longer than middle femora.
(13) Male genital segments protruding from abdominal end; male parameres not visible externally.

The general structure and especially characters 2, 5, 6, 7, 9, and 10 place the insect in the gerromorphan family Veliidae (Andersen, 1982, 1998). The combination of the characters 8 and 10 are diagnostic for the subfamily Microveliinae. There are about 30 extant genera of this subfamily most of which are keyed out by Andersen (1982: 419). Using this key, the fossil species is identified as belonging to the genus *Microvelia* s. lat. which is worldwide in distribution with more than 200 species. With the exception of the northern temperate regions, the taxonomy of the genus is chiefly based on isolated descriptions of species and largely outdated revisions and reviews. This is in particular the case for the numerous *Microvelia* species known from the Neotropical region. A key character for the fossil species is the bicolored fore wings. Most microveliines have either unicolored, dark wings or dark wings with a number of pale spots.

Polhemus and Polhemus (1991) gave an excellent review of the veliid fauna of bromeliads and keyed out all species known to occur in this type of habitat. Using this key (Polhemus and Polhemus, 1991: 205–207), the small size (less than 2.5 mm), tarsal formula (1:2:2), brownish ground color, and white basal marking on the hemelytra of the fossil species, perfectly match the characters of *Microvelia laesslei,* first described from Jamaica by Drake and Hussey (1954: 134–136). The macropterous form of this species (sex not stated in the original description) measures 2.30 mm (length) and 0.85 mm (width). Thus, even when allowing for sexual size differences, *M. laesslei* is larger and more robust than the fossil species. In addition, the pronotum of *M. laesslei* is uniformly brown or reddish-brown, without a pale transverse marking anteriorly. The third and fourth antennal segments are subequal in length, whereas the fourth segment is distinctly longer than the third segment in the fossil species. *Microvelia polhemi* n. sp. is otherwise very similar to *M. laesslei* in those characters where the state of preservation of the fossil makes a comparison possible.

There are two additional specimens belonging to the genus *Microvelia* in the material of Dominican amber insects deposited at AMNH. One specimen is a macropterous male with rather elongate body, length 1.8 mm; antennae long and slender, and genital segments relatively small; fore tibia apparently without a grasping comb. The other specimen is a very small macropterous male, length 1.35 mm, with relatively short and stout antennae and large genital segments. Further studies, including

comparisons with extant Neotropical species of *Microvelia,* are necessary for assessing the relationships of these fossil water striders.

**Biology and ecology.** *Microvelia laesslei* Drake and Hussey (1954) was described from both micropterous and macropterous specimens collected from plants belonging to the family Bromeliaceae by Albert M. Laessle, University of Florida, in August and early September, 1952, at Christiana, Juan de Bolas (elevation 2,500 feet), and Mocho (elevation 2,000 feet), Jamaica. These adult specimens, together with numerous nymphs of all ages, were collected by Laessle in an investigation of the fauna of the rain-water pockets of Jamaican bromeliads. The circumstances of these findings are described in the following citations from the original description by C. J. Drake and R. F. Hussey:

"Dr. Laessle investigated numerous species of bromeliads in various parts of Jamaica. The *Microvelia* was found principally in *Aechmea paniculigera* Griseb., and in species of *Hohenbergia* and *Vriesia.* These are large bromeliads, sometimes holding as much as two liters of water; the *Aechmea* has relatively few leaves, and some of its individual axils may contain nearly one-third liter. The water in all these plants abounded with small arthropods of various kinds, among which were entomostracans, and larvae of helodid beetles, mosquitoes, and Chironomidae. These afforded a plentiful supply of food for *Microvelia.*"

"The *Aechmea* and the *Hohenbergia* species are widely distributed in Jamaica, occurring often as epiphytes, but also growing directly upon rocks in exposed situations. The *Microvelia,* however, was found in them only in the central and west-central parts of the island, and only at elevations of 2,000 feet or more. *Microvelia laesslei* is not restricted to any one area in the plant, but occurs in the water pockets from the outermost to the innermost whorl of leaves."

"Even the youngest nymphs are strikingly banded with white across the basal segments of the abdomen, simulating the broad white marks on the hemelytra of the fully winged form, or the white wing pads of the micropterous form. No truly apterous individuals have been seen." (Drake and Hussey, 1954: 136).

Since the male of *M. polhemi* n. sp. is fully winged, it may have been caught in a flow of resin excuding from the Dominican amber-tree (*Hymenaea protera)* while it was dispersing by flight between habitats. Although the amber fossil does not provide any direct evidence for the way it lived 15–30 million years ago, its close relationship to a bromeliadicolous species strongly suggests that the small water strider lived in this type of habitat. The reconstruction of the ancient Dominican amber-forest displayed by David Grimaldi in his superb book "Amber—Window to the Past" (Grimaldi, 1996: 101), indicates that the *Hymenaea*-trees harbored epiphytic bromeliads even then. Grimaldi further writes: "Bromeliads were nestled among the branches of the Dominican amber trees themselves. A species of butterfly in Dominican amber (a metalmark) and its caterpillars probably fed upon the bromeliads. Living in the little ponds that accumulate in the center of the bromeliads, no doubt, were mosquitoes, predacious diving beetles, and perhaps even the small frogs found preserved in the amber." (Grimaldi, 1996: 100, 105). It now seems justified to add *M. polhemi* n. sp. to this ancient animal community.

Polhemus and Polhemus (1991) gave an excellent account of the biology and ecology of veliids living in pockets of rain-water in plants belonging to the Bromeliaceae. "The veliid species that we have collected in bromeliads are usually

found between the rather tightly fitting leaves in the center of the plant which trap rainwater in a series of deep pockets, and never occur in bromeliads that lack such water pockets. Among the taxa involved, the *Paravelia* species appear to prefer ground dwelling bromeliad species, while the *Microvelia* species have been taken from both terrestrial and arboreal bromeliads. *Paravelia* and *Microvelia* are in different subfamilies (Veliinae and Microveliinae respectively), so it is clear that adaptation to the bromeliad habitat has occurred on at least two separate occasions. Even so, there are convergent similarities in appearance among all bromeliadicolous species. The macropterous forms possess bright yellow or white spots on the hemelytra, and in the genus *Paravelia* only this morph is known. In *Microvelia* every known bromeliad inhabiting species has in addition either a micropterous or an apterous morph with light markings dorsally in the same position as the light wing spots of the winged morph; in *M. laesslei* these are white micropterous wing pads, in *M. distanti* they are a combination of light colored regions of the integument and silvery pubescent areas, and in *M. ancona* and *M. oaxacana* they are simply bright silvery pubescent areas." (Polhemus and Polhemus, 1991: 204–205).

The difficulties involved in locating and collecting these insects are vividly described: "We have found that bromeliadicolous veliids are generally not evenly distributed within a patch of bromeliads, but instead tend to aggregate in certain individual plants. While most bromeliads searched will contain only one or two insects, or more commonly none at all, occasional plants are found which contain up to a dozen. In such preferred plants it is often possible to see one or more specimens in a water pocket using a flashlight, and once located they can sometimes be seen even in ambient light, moving about as ghost-like creatures on the water-surface, with only the bright markings visible. The ground dwelling bromeliads that harbor these veliids are often rather large plants which may occur either on the forest floor or on sheer cliffs where collecting is distinctly hazardous. In many instances the plants must be cut off near the base and the leaves peeled away one at a time while each is searched for the veliids, which once exposed run rapidly over the leaf surfaces and attempt to hide in crevices, or move to the dark undersides of the remaining leaves. The most effective way to collect them under such circumstances is by use of an aspirator, with one person dismembering the bromeliad while a second stands ready to suck up the escaping insects." (Polhemus and Polhemus, 1991: 205).

**Distribution and biogeography.** The genus *Microvelia* is cosmopolitan but is most species-rich in tropical regions of the World (Andersen, 1982). *Microvelia polhemi* n. sp. is undoubtedly closely related to *M. laesslei* from Jamaica. Most insects known from Dominican amber can also be assigned to taxa which show distinct affinities to species found in the Caribbean and adjacent areas today (Poinar, 1992; Grimaldi *et al.,* 1993; Grimaldi, 1996; Michelsen, 1996). Gerromorphan bugs known from Dominican amber, however, also include forms not included in the extant fauna of these areas. The water strider *Electrobates spinipes* Andersen and Poinar (1992) cannot be classified in any extant subfamily of the Gerridae and has no close relatives in the Caribbean today. Finally, a species belonging to the marine water strider genus *Halovelia* (Veliidae), at present confined to the Indo-West Pacific, was recently described from Dominican amber (Andersen and Poinar, 1998).

**Phylogeny and fossil history.** Water striders and other semiaquatic bugs (Hemiptera-Heteroptera, Gerromorpha) comprise about 1,600 extant species classified in eight

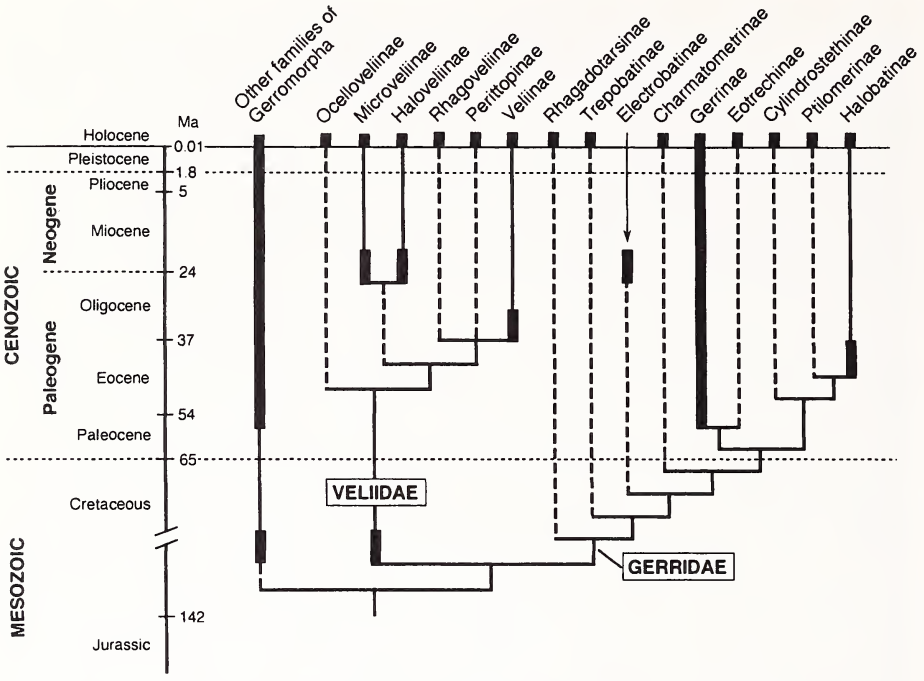



Fig. 4. Phylogenetic tree for the subfamilies of Veliidae and Gerridae (Gerromorpha). Temporal distribution of fossils indicated by heavy branches; unbroken branches denote range extensions inferred from fossils; broken branches denote range extension inferred from sister group relationships. (Modified from Andersen, 1998: fig. 80).

families. The phylogenetic relationships between the gerromorphan families and subfamilies were analyzed and discussed by Andersen (1982). So far, about 30 fossil species belonging to six families have been described or recorded, spanning more than 120 million years of geological history (Andersen, 1998). Although the fossil record of water striders is immensely imperfect, the available fossils provide useful insights into the evolutionary history of the group. By applying cladistic principles and methods, fossil taxa can in most cases be placed in phylogenies (cladograms) together with their extant relatives. Cladograms calibrated against the fossil record yield phylogenetic trees which can be used to estimate minimum divergence time of extant monophyletic groups (clades).

The phylogenetic tree (Fig. 4) depicts the relationships between the subfamilies of the large gerromorphan families Veliidae and Gerridae and the range of fossil forms belonging to these groups. So far, only few fossils have been classified as belonging to the family Veliidae. *Electrovelia baltica* Andersen (1998) from Baltic amber (Eocene/Oligocene) was classified in the Veliinae, setting a minimum age for this subfamily to 40–35 myr. By range extension, the same minimum age can be assigned to the subfamilies Rhagoveliinae and Perittopinae, both without known fossils. So far, *Electrovelia* is the oldest fossil taxon which can be classified in the Veliidae with absolute certainty. However, the family probably originated long before

as indicated by possible veliid fossils from the Lower Cretaceous of Australia (Jell and Duncan, 1986).

*Halovelia electrodominica* Andersen and Poinar (1998) was described from Dominican amber (Oligocene/Miocene). When the characters of this species were added to a character data matrix based on extant species, the fossil species assumed a position as the most basal branch of *Halovelia.* Thus, the minimum age of this genus, as well as of the subfamily Haloveliinae, is 30–15 myr (Fig. 4). Since the subfamily Microveliinae is the sister group of the Haloveliinae, both clades can be assigned the same minimum age (Andersen, 1998: 108). The fossil veliids recorded and described in the present paper suggests that the genus *Microvelia* as well as the subfamily Microveliinae is at least 30–15 myr old.

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